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Extension of the Recorded Host Range of Caribbean Christmas Tree Worms (*Spirobranchus* spp.) with Two Scleractinians, a Zoantharian, and an Ascidian

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Caribbean Christmas tree worms (Annelida: Polychaeta: Serpulidae: *Spirobranchus*) are considered host generalists in their associations with anthozoan (Scleractinia) and hydrozoan (*Millepora*) stony corals [1–4]. As planktonic larvae, they settle on coral surfaces and start secreting a calcareous tube to be used as a dwelling. This tube usually becomes overgrown by the host coral (except for its opening) and may get encapsulated deep inside the coral skeleton. In this manner, the well-protected worms grow and survive predation [5] and other hazards, allowing them to live for over four decades [6]. When the host corals are overgrown by other organisms, such as octocorals and sponges, these may act as secondary hosts [7,8].

The long lists of Caribbean host species suggest that the recorded number has reached a maximum [1–4]. However, recent surveys (2015–2019) in the southern and eastern Caribbean, as well as in the Greater Antilles, enabled us to establish new records of two primary hosts (scleractinians) and two secondary hosts (a zoantharian and an ascidian).

The coral–worm associations occurred in shallow subtidal water (<4 m depth), with *Pseudodiploria clivosa* (Ellis & Solander, 1786) hosting *Spirobranchus giganteus* (Pallas, 1766) at St. Eustatius (Figure 1) and *Favia fragum* (Esper, 1795) hosting both *S. giganteus* (Figure 2a–c) and *S. polycerus* (Schmarda, 1861) (Figure 2d) at Bonaire. The secondary host observations, both for *S. giganteus*, involved the zoantharian *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860) at Puerto Rico (Figure 3) and the ascidian *Trididemnum solidum* (Van Name, 1902) at Bonaire and Curaçao (Figure 4). *Palythoa caribaeorum* represents a first record as a secondary host for a species of the order Zoantharia. Until now, the only other anthozoan secondary hosts were species in the order Alcyonacea (subclass Octorallia) [7], whereas *T. solidum* represents an entirely new host phylum, viz. Chordata. The only other non-anthozoan secondary hosts known to date are sponges (Porifera) [8].

The two new scleractinian hosts are both typical for shallow subtidal water near the shoreline (<4 m depth), where a lack of previous surveys may explain why they have not previously been reported. The new records of secondary hosts are remarkable because these encrusting animals are known to be aggressive in competition for space with scleractinians by allelopathy [9,10] and can be

abundant on shallow reef flats and slopes, where they usually outcompete and kill scleractinian corals by overgrowing them [9,10]. In both cases, the Christmas tree worms survive by withstanding this overgrowth and maintain an open space near the tube opening (Figures 3d, 4b, 4e).

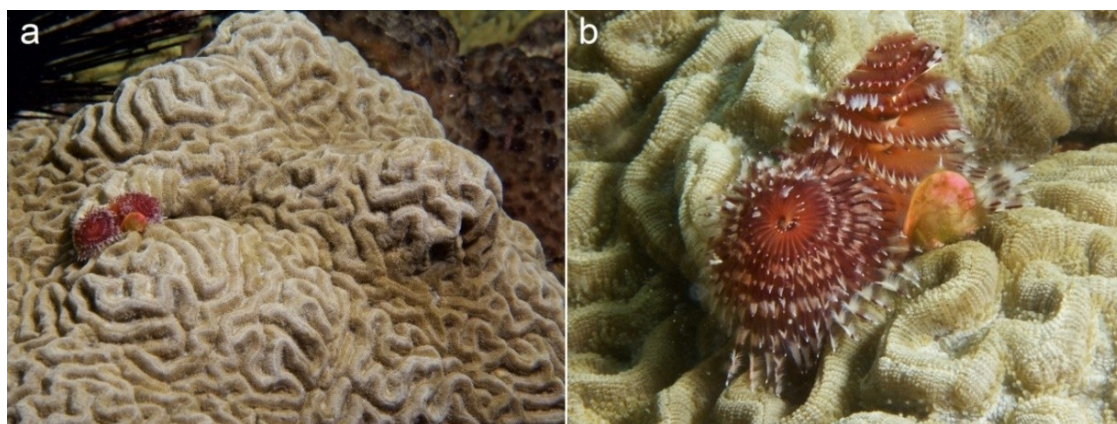


Figure 1. A coral of *Pseudodiploria clivosa* at 2 m depth, Scubaqua house reef (17°28'56" N 62°59'20" W), St. Eustatius, Eastern Caribbean (2015) hosting *Spirobranchus giganteus*: (a) overall view and (b) close-up.

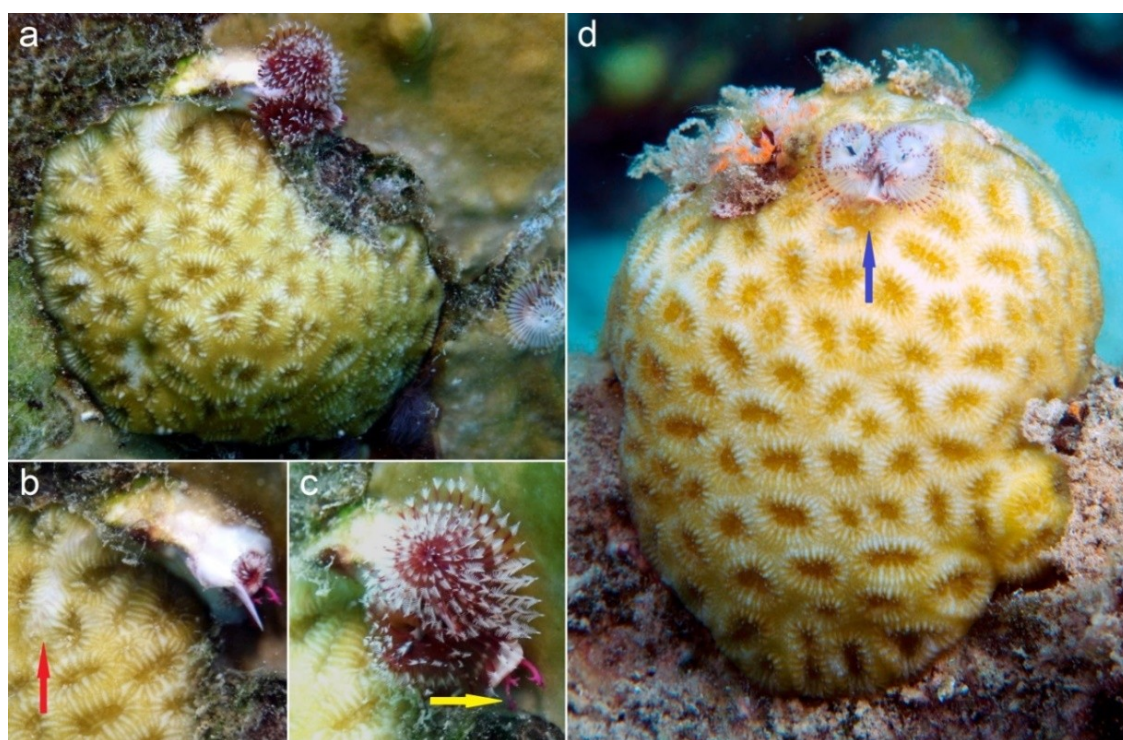


Figure 2. *Favia fragum* hosting *Spirobranchus* spp. at 3–4 m depth, dive site “Front Porch” (12°09' 54" N 68°17'12" W), Bonaire, Southern Caribbean (2019). (a–c) *Spirobranchus giganteus*: overall view (a), overgrown tube section indicated by red arrow (b); antler-shaped opercular spines showing dark pink coloration indicated by yellow arrow (c). (d) *Spirobranchus polycerus*: two individuals, one showing white spines on its operculum (blue arrow).

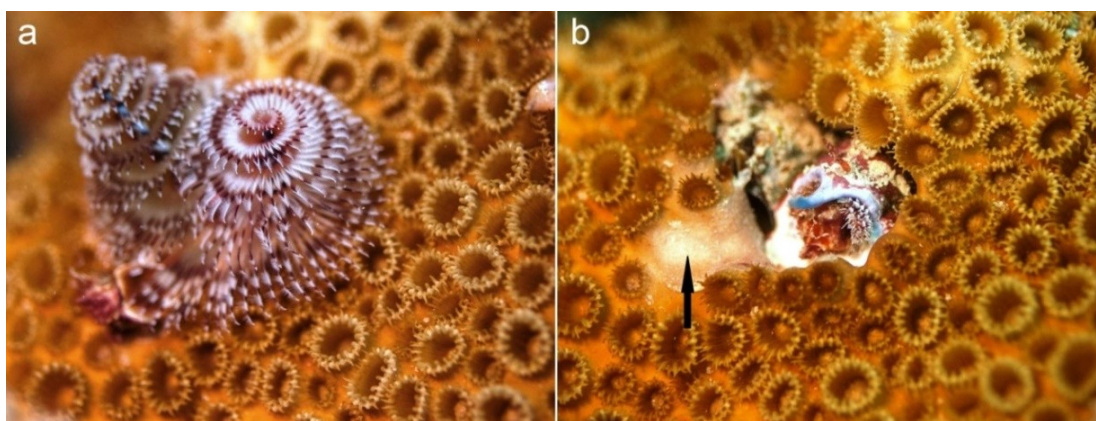


Figure 3. *Palythoa caribaeorum* acting as a secondary host for *Spirobranchus giganteus* at 5 m depth, Cayo Media Luna (La Parguera Natural Reserve), Puerto Rico, Greater Antilles (2017): (a) worm extended and (b) retracted, showing the tube opening surrounded by dead coral; damage to the zoantharian host caused by the operculum of the extended worm indicated by a black arrow.

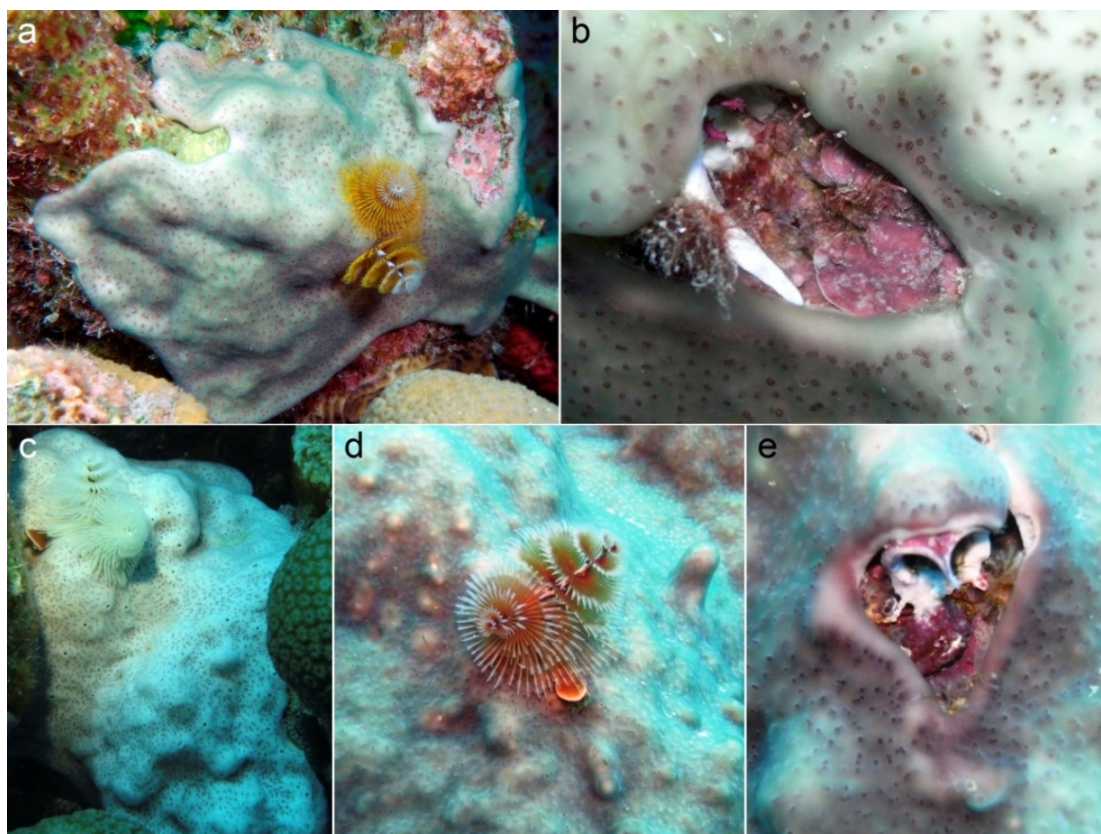


Figure 4. *Trididemnum solidum* acting as a secondary host for *Spirobranchus giganteus* in the Southern Caribbean: (a,b) dive site “Thousand Steps” (12°12'39" N 68°19'17" W), Bonaire (2019); (c) Marie Pampoen (12°05'31"N 68°54'27"W), Curaçao, 12 m depth (2017); (d,e) Daaibooi Bay (12°12'41"N 69°05'13"W), Curaçao (2017). Extended worms (a,d) and the same individuals retracted, showing an open space in front of the worm tube mouth (b,e).

Our new host records confirm two Caribbean Christmas tree worms as generalist symbionts capable of infesting a large spectrum of host corals. They are also strong survivors when their primary hosts become overgrown by more aggressive competitors for space. Previous host records mostly concern *S. giganteus* [1–4], but here we also report a new host coral for *S. polycerus*. This worm species occurs in shallow water (<4 m depth) [5], whereas *S. giganteus* is commonly found down to 40 m depth [1]. Both *Spirobranchus* species can easily be distinguished [5], as *S. giganteus* shows long dark pink opercular spines (Figure 2c), whereas those of *S. polycerus* are short and white (Figure 2d).

Furthermore, *S. giganteus* may be larger than *S. polycerus* [5] and usually shows six to seven (maximum eight) whorls in its branchial spires, whereas *S. polycerus* has two to three (maximum five) [11]. Our observations suggest that future surveys may discover other hosts for both *Spirobranchus* species with the possibility of more host overlap. Whether such host sharing is related to their phylogenetic affinities or to ecological similarities (e.g., overlapping bathymetric distributions) is an open question that merits assessment.

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